

MIOCENE AND PLIOCENE MOLIDAE
(*RANZANIA*, *MOLA*) FROM MARYLAND,
VIRGINIA, AND NORTH CAROLINA
(PISCES: TETRAODONTIFORMES)

Robert E. Weems

Abstract.—Three species of fossil molid fish (Tetraodontiformes) are represented in the Miocene and Pliocene deposits of the central Atlantic Coastal Plain. Two species belong to the genus *Ranzania* (*R. grahami* and *R. tenneyorum*) and one belongs to the genus *Mola*. Premaxillary beaks were found to be best suited for osteologically defining species and genera in this family. Osteological definitions for the living and fossil genera and species in this family are proposed based principally on the character states present in the premaxillary elements.

Fossil molid remains were first recognized in 1883, when Van Beneden described the upper and lower "beaks" of "*Orthogoriscus chelonopsis*" from Belgium. Later, Leriche (1907) pointed out that Van Beneden already had described two dermal bones of molids in 1881, but that he had incorrectly assigned them to the genus *Pagrus*, as *P. pileatus* and *P. torus*. Because Leriche considered all of these materials to belong to a single species, he therefore called all of these specimens *Orthogoriscus pileatus* on the basis of page priority. In 1926, Leriche figured more material recovered from the Brussels basin and compared it to the living species *Mola mola* (then usually called *Orthogoriscus mola*). Leriche decided that all of his fossil material constituted a single species which was collectively distinct from the modern species. More recently, Van Deinse (1953) described some dermal bones of a molid from the upper Miocene strata of the Netherlands which he also chose to refer to *Mola pileata*. These Miocene dermal bones are quite comparable to the material Van Beneden and Leriche described, especially since dermal bones are highly variable in shape in the living *Mola mola* (Harting 1864, cited in Van Deinse 1953). Romer (1966:361) listed the genus *Mola* as occurring in the Tertiary of South America, but no other reference to such an occurrence was located. Apart from this one reference, all fossil specimens of molids reported in the literature have been from Miocene strata of France, Netherlands, and Belgium, and all of this material has been referred to a single fossil species of the extant genus *Mola*.

Berry (1941) unknowingly described a molid premaxillary beak from the upper part of the Calvert Formation of Virginia; he considered it to be the fused dentaries of the sea turtle *Syllomus*. D. H. Dunkle brought this error to my attention and it was footnoted in my paper on Calvert sea turtles (Weems 1974). Because only a footnote was published, the true nature of this premaxillary beak is still not widely recognized by ichthyologists. Since Berry's paper, much more molid material has been collected from the Calvert and from the overlying Choptank Formation. Much of this material has good stratigraphic control. A large selection of premaxillary beaks are known from the upper Calvert which can be used to determine the degree of variability in the premaxillary beaks of what was probably

a single genetic population. Three other specimens, one from Calvert-age beds in central Virginia, one from the Choptank Formation of Maryland, and the third from the Yorktown Formation of North Carolina, clearly fall outside of the range of variability seen in the upper Calvert population of specimens. This indicates that a major revision of the taxonomy of the fossil members of this family is warranted and that two new species of molids can be recognized.

Material

The following specimens were used for comparisons made in this paper. "Zones" are from Shattuck (1904):

- 1) AMNH 1679. Premaxillary beak. Calvert Formation, upper "zone" 11, "zone" 12, or lower "zone" 13, Horsehead Cliffs, Westmoreland State Park, Westmoreland County, Virginia. Charles T. Berry, 9 Jun 1940 (see Berry 1941).
- 2) USNM 16363. Premaxillary beak. Calvert Formation, Chesapeake Beach, Calvert County, Maryland. William Palmer.
- 3) USNM 16364. No data.
- 4) USNM 16615. Premaxillary beak. Calvert Formation, Scientists Cliffs, Calvert County, Maryland. W. E. Salter, 1941.
- 5) USNM 16668. Premaxillary beak. Calvert Formation, Scientists Cliffs, Calvert County, Maryland. Mr. Foshag and Remington Kellogg, 1941.
- 6) USNM 16743. Premaxillary beak. Calvert Formation, "zone" 11, Scientists Cliffs, Calvert County, Maryland. L. P. Schultz, 1943.
- 7) USNM 186982. Dentary beak. Calvert Formation, "zone" 11, about 2 feet above shell layer, 1.7 miles south of Plum Point, Calvert County, Maryland. R. Lee Collins, 6 Jul 1936.
- 8) USNM 186983. Premaxillary beak. Choptank Formation, "zone" 19, just north of Bay Haven Camp, Calvert County, Maryland. R. Lee Collins, 8 Sep 1933.
- 9) USNM 186984. Dentary beak. Found on beach at Randle Beach. Lauck W. Ward, Aug 1969.
- 10) USNM 186986. Premaxillary beak, dentary beak, dorsal armor shield, nasal plate, jugular plate, and branchial arch or vertebral spine fragments. Calvert Formation, upper "zone" 11, Horsehead Cliffs, Westmoreland State Park, Westmoreland County, Virginia. R. E. Weems, Mar 1967.
- 11) USNM 265391. Fragmentary premaxillary beak. Calvert Formation, upper "zone" 11, Stratford Cliffs, Westmoreland County, Virginia. James Kaltenbach.
- 12) USNM 265392. Premaxillary beak. Calvert Formation, in the local basal phosphate horizon of Calvert Formation, Gravett's Mill Pond, King William County, Virginia. R. E. Weems, Dec 1969.
- 13) USNM 265393. Fused dentary beak. Calvert Formation, upper "zone" 11, 4 feet above beach, Stratford Cliffs, Westmoreland County, Virginia. Robert E. Weems, around 1970.
- 14) USNM 265394. Premaxillary beak. Calvert Formation, upper "zone" 11, 4 feet above beach, Stratford Cliffs, Westmoreland County, Virginia. R. E. Weems, Mar 1970.
- 15) USNM 265395. Fragmentary premaxillary beak. Calvert Formation, "zone"

- 12, 6 feet above beach, south corner of second bluff north of Parker Creek, Maryland. James Kaltenbach.
- 16) USNM 265650. Fragmentary premaxillary beak. Yorktown Formation, Lee Creek Mines, Aurora, North Carolina.
 - 17) USNM 265651. Isolated dermal plates. Calvert Formation, "zone" 12, Parkers Creek, Calvert County, Maryland. Collector unknown, 20 Apr 1935.
 - 18) USNM 265653. Molid jugal plate. Probably Calvert Formation, Scientists Cliffs, Calvert County, Maryland. Collector Walter Simonson.
 - 19) USNM 291211. Fragmentary premaxillary beak. Yorktown Formation, Lee Creek Mines, Aurora, North Carolina.
 - 20) USNM 336431. Small premaxillary beak. Calvert Formation, "zone" 10, Plum Point, Calvert County, Maryland. David O. Bohaska, 15 Oct 1983.

Description

Of the above-cited specimens, five include much or all of the premaxillary beak and also come from either upper "zone" 11 of the Calvert or possibly from "zone" 12 or lower "zone" 13. Three others almost certainly come from this same interval. These specimens occur within a narrow stratigraphic range, so it is reasonable to compare them to see if they represent more than a single population. The angle of these beaks are all within the rather narrow range of 77° to 88° , with a mean value of 84.5° and a standard deviation of $\pm 2^{\circ}$. The beaks vary considerably in total size, but this is to be expected due to wide differences in the age of individuals at death. The most variable character is the ratio between the beak length and the length of the bony palate that lies behind the beak. Even here, however, the changes are readily correlated with size and can be ascribed to age variation within a single species (Fig. 1).

Except for USNM 336431, each specimen is toothless in the region of the anterior biting edge of the beak, but farther back on the roof of the mouth the bony palate region contains three poorly defined rows and clusters of teeth sharply demarcated from the toothless area (Figs. 1, 3D, 6D, 7B). The teeth are poorly developed and show no clear sign of enamel covering. The bony palate above and behind the tooth-bearing region consists of a large mass of bone which acts as a brace for the teeth. This is variably developed, but generally is more massive in larger specimens.

One specimen within this population (USNM 186986) is a partial skeleton of a single large individual. This specimen includes the premaxillary beak, the dentary beak, the nasal plate, the jugular plate, a large sheet of dermal armor, and poorly ossified bones possibly representing branchial arch supports or vertebral spines (Figs. 3–5). This material constitutes most of what could reasonably be expected to be fossilized in a mold. This specimen and the previously discussed isolated premaxillary beaks from the upper Calvert Formation can be referred to a single species that is variable within well-defined limits. Collectively, these beaks all differ from the described European specimens in the massive development of the tooth-bearing bony palate behind the beak (Fig. 7). Such a palate is absent in all but one of the specimens described by Leriche and in the living *Mola mola*. Therefore, the upper Calvert population represents a single species that is distinct from the one described European mold species.

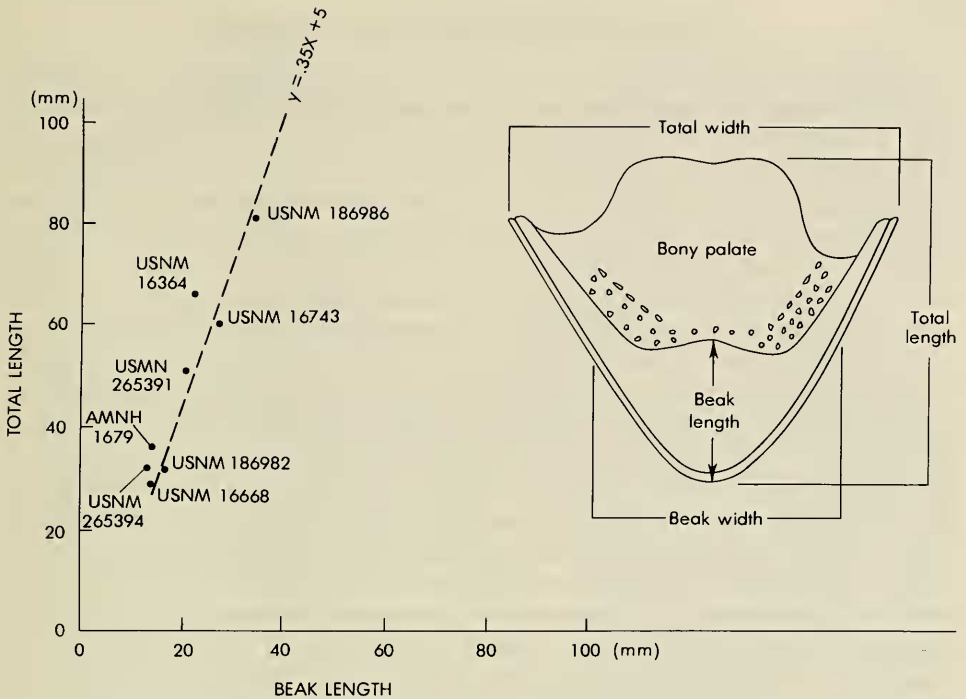


Fig. 1. Graph showing the distribution in size of specimens of *Ranzania grahmi* n. sp. from the upper Calvert Formation. Although total length and beak length vary greatly (see inset), the ratio of these two values are related by the simple algebraic relationship $y = 0.35X + 5$ (dashed line). Thus, these specimens probably represent different growth stages within a single population.

Three other premaxillary beaks from Maryland, Virginia, and North Carolina fall well outside the range of variation seen in the upper Calvert specimens. One specimen comes from beds in central Virginia that appear to be equivalent to the upper Plum Point Marl Member of the Calvert Formation (L. W. Ward, written communication, 1983). This beak differs from the previously described specimens in the development of three pairs of well-defined tooth rows on the oral surface of the palate (Fig. 7D). These are quite distinct, unlike the poorly developed tooth rows of the specimens already considered. The other two beaks, a premaxillary beak from "zone" 19 of the Choptank Formation of Maryland (Fig. 7C), and a premaxillary beak from the Yorktown Formation of North Carolina (Figs. 6A, B), have lost all trace of the tooth rows and most of the mass of bone above the tooth rows. Their conformation is most like that of the European molids that have been described in the literature. In these two kinds of beaks we can see (1) an earlier morphological stage where teeth are better developed than in the previously considered upper Calvert population and (2) a later morphological stage in which the teeth are essentially gone, closely approaching the condition seen in the all but toothless living *Mola mola*. Since the toothless beaks are still better ossified than those of the living *M. mola*, they are best referred to *M. chelonopsis* and not to either of the living species. The beak with well developed tooth rows appears to represent a second new species of molid.

Osteology of the Living Genera of Molids

Although all fossil molid materials previously have been referred to the genus *Mola*, there are three extant genera in the family (Tyler 1980). Fraser-Brunner (1951) considered *Mola* to include two species (*M. mola* and *M. ramsayi*), but Tyler (1980) seems unconvinced that the two species are distinct. Both Tyler and Fraser-Brunner consider *Ranzania* and *Masturus* to be monotypic. Several papers have appeared on the anatomy of these fishes (for *Mola*: Gregory and Raven 1934; for *Ranzania*: Raven 1939a; for *Masturus*: Gudger 1937a, b; Raven 1939b), but the only paper that has dealt with the dental apparatus of any of these fishes is Tyler (1980). Although Tyler notes a crowded tooth battery in young *Mola*, study by the present author of adult skeletal remains has shown no instance in which distinct teeth are rooted in the bony portion of either the upper or lower beaks. Apparently the teeth are entirely embedded in cartilage in the living adult fish. Study of whole specimens of *Ranzania* by the author has shown that this genus possesses well developed rows of teeth which move past each other as the fish chews, apparently producing a shredding and chopping action (e.g., USNM 75155; ANSP 106723) (Fig. 2). *Ranzania* has been reported to eat only littoral seaweed (Barnard 1927), so the utility of this dental apparatus seems obvious. Only two specimens of *Masturus* could be located; neither was available for dissection (USNM 5704; AMNH 15962). Observation of the mouth, however, revealed a battery of rounded pavement teeth (Fig. 2) reminiscent of those developed in pycnodont fishes and the living drumfish (*Pogonias*). The conformation of the teeth in the premaxillary beak differs somewhat from that shown in Tyler (1980:387), possibly due to age or size variation, but the dentary tooth battery in the specimens I observed agree well with the one figured by Tyler (p. 389). Although I could not observe if a bony mouth roof is present in *Masturus*, the figure of the skull of *Masturus* in Tyler (1980) suggests that one is possibly present. No such mass is present in the very cartilaginous *Mola*. Of the three living genera, only *Ranzania* has an extensive dermal skin external covering of regularly polygonal, bony armor plates; in both *Masturus* and *Mola* there are only scattered dermal patches bound in a cartilaginous sheet (Fraser-Brunner 1951, Tyler 1980).

Taxonomy of the Miocene and Pliocene Molids

From the foregoing descriptions, it is clear that only the Choptank and Yorktown premaxillary beaks can be referred properly to the genus *Mola*. The presence of regular rows of shredding teeth and a large mass of bone reinforcing the dental battery readily place the central Virginia beak in the genus *Ranzania*. The upper Calvert specimens afford a somewhat intermediate state between *Ranzania* and *Mola*, but since the bone reinforcing the dental battery is retained and an extensive bony dermal armor (albeit composed of irregular rather than polygonal plates) is retained, this form as well is best considered still to belong within the genus *Ranzania*. It is obvious, however, that this species had evolved far in a direction toward the character states present in the living genus *Mola*.

Since the jugular and nasal bones are quite variable in shape and show no major change in form and shape from the upper Calvert population of *Ranzania* through the modern *Mola mola*, they are of little more than familial taxonomic value.

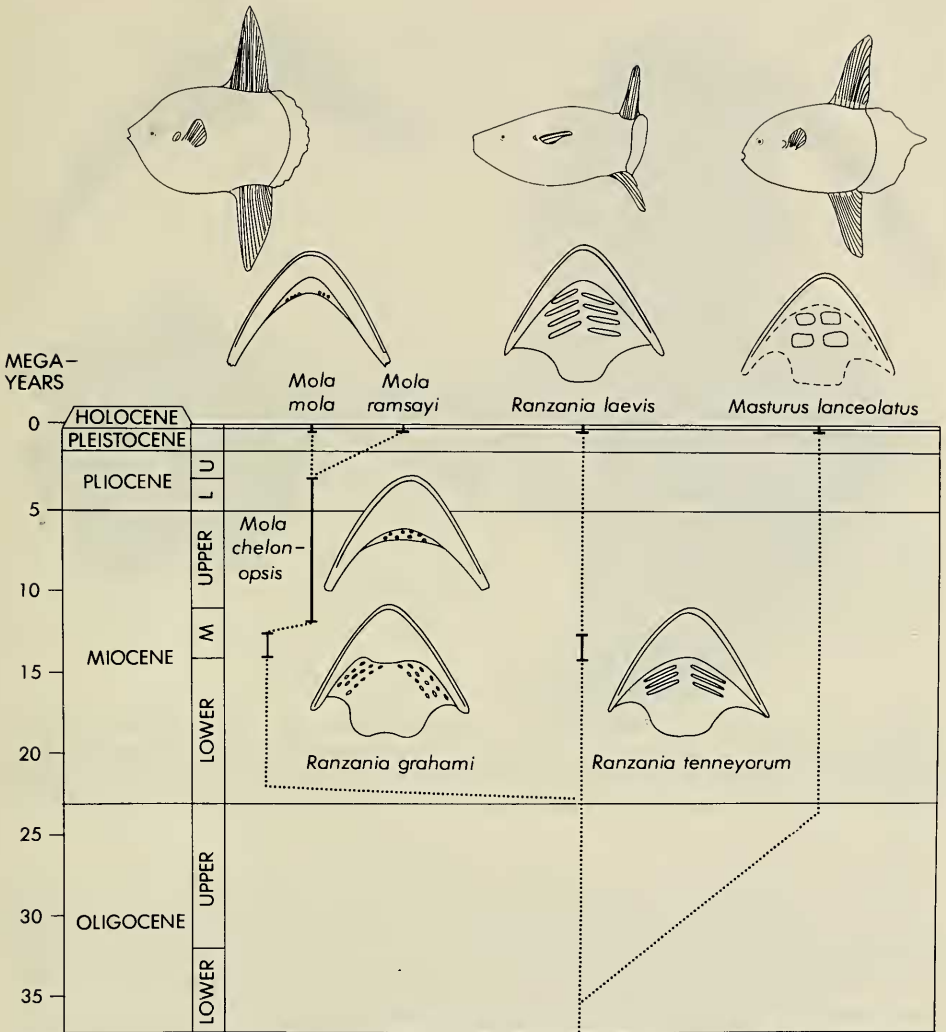


Fig. 2. Morphology and oral characteristics represented in the various fossil and living species of the family Molidae. Age ranges (solid lines) and probable phyletic pathways (dotted lines) are indicated.

Therefore, the species described by Van Beneden as *Pagrus pileatus* and *Pagrus torus* are considered to be each a nomen dubium; they could belong to any of at least three species of fish. Only "*Orthogoriscus chelonopsis*" shows enough characters to merit designation as a type, and the proper name for this species should be *Mola chelonopsis*. This specimen is quite comparable to the nearly toothless species present in the Choptank and Yorktown (cf. Leriche 1926). The upper Calvert species is undescribed, so the name *Ranzania grahami* is proposed after Robert A. Graham, who has accompanied the author on numerous fossil molid collecting trips. The central Virginia species also is undescribed, and the name *Ranzania tenneyorum* is proposed after Eleanor and Wilton Tenney, who also

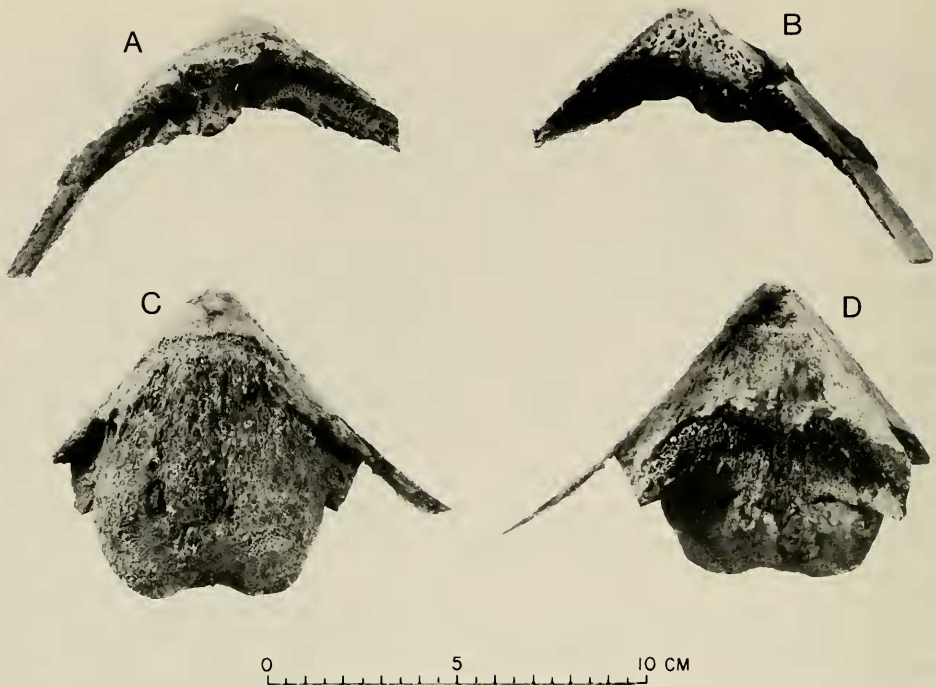


Fig. 3. Dentary and premaxillary beaks of *Ranzania grahami* n.sp. (type), USNM 186986. A, Dentary beak, ventral (aboral) view; B, Dentary beak, dorsal (oral) view. Note the notch cut in the right dentary by a predator's tooth (dark shadow) and the piece of bone displaced outward by this injury; C, Premaxillary beak, dorsal (aboral) view; D, Premaxillary beak, ventral (oral) view.

spent considerable time collecting with the author on the trips when mold remains were found. Because *Masturus* is so poorly known, it cannot be adequately defined yet in osteological terms. However, the presence of rounded crushing teeth is obviously a key distinguishing character. Osteologically the three recognizable living and fossil species of *Ranzania* can be defined as follows:

Ranzania Nardo, 1840

Ranzania Nardo, 1840:10, 105 (type-species: *Ranzania typus* Nardo (= *Ostracion laevis* Pennant) by Whitley 1933).

Generic diagnosis.— External dermal coating of polygonal plates, internal skeleton largely cartilaginous except for premaxillaries and dentaries fused respectively into upper and lower beak. Upper beak posteriorly containing rows or patches of teeth fused against thick mass of bracing bone overlying roof of mouth.

Range.— Middle Miocene to Holocene.

Ranzania laevis (Pennant, 1776)

Species diagnosis.— In addition to generic characters, this species shows a regularly polygonal array of dermal plates. Teeth occur in four discrete intermeshing



Fig. 4. Ventral view of the dorsally located dermal armor shield of *Ranzania grahami* n.sp. (type), USNM 186986.

rows on both the dorsal and ventral surfaces of the mouth, ventral row not attached to a bony shelf.

Range.—Holocene.

Ranzania grahami, new species

Figs. 3–5, 6C–D, 7A–B, 8

Holotype.—USNM 186986, Premaxillary beak, dentary beak, dorsal armor shield, nasal plate, jugular plate, and branchial arch or vertebral spine fragments; Calvert Formation, upper “zone” 11, Horsehead Cliffs, Westmoreland State Park, Westmoreland County, Virginia; R. E. Weems, Mar 1967.

Species diagnosis.—In addition to generic characters, dermal coating made of very irregularly-shaped polygonal plates. Teeth present but in poorly defined rows and patches that are rooted directly to the palatal bracing bone. In the one known very young premaxillary beak specimen (less than 20 mm length), the anterior beak region may contain up to six pairs of tooth ridges crowded against the front of the beak, followed posteriorly by the irregular tooth rows on the bony palate typical of this species. Apparently the anterior six rows wear out with age, leaving this region toothless in larger individuals. Nasal plate and jugular plate similar to those of living *Mola mola*.

Range.—Lower middle Miocene.

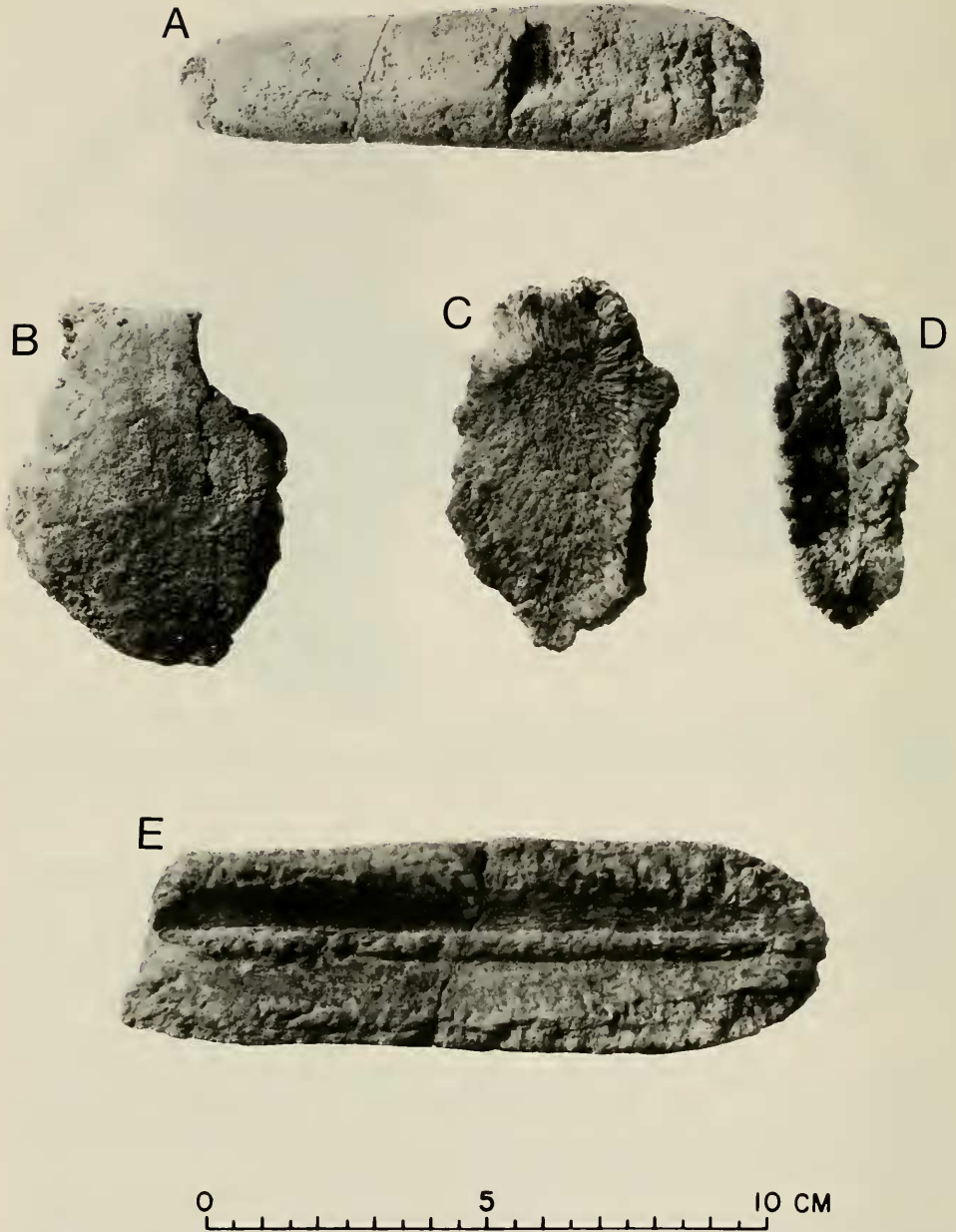


Fig. 5. Isolated dermal bones of *Ranzania grahami*. A, Jugular plate (USNM 265651); B, Nasal plate (USNM 186986, type); C, Dermal element (USNM 186986, type); D, Fragmentary jugular plate (USNM 186986, type); E, Jugular plate (USNM 265653).

Ranzania tenneyorum, new species

Fig. 7D

Holotype.—USNM 265392, premaxillary beak; Calvert Formation, in the local basal phosphate horizon of Calvert Formation, Gravett's Mill Pond, King William County, Virginia; R. E. Weems, Dec 1969.

Species diagnosis.—Based solely on the fused premaxillaries. Beak small, with three well developed pairs of tooth rows present behind it which are located on a bony shelf well below the level of the palatal bracing bone, so that there is a well developed notch behind the tooth rows. Other premaxillary beak characters as in genus.

Range.—Lower middle Miocene.

Mola Koelreuter, 1770

Mola Koelreuter, 1770:337 (type-species: *Mola aculeata* Koelreuter (= *Tetraodon mola* Linnaeus, juvenile) by Jordan, 1885).

Generic diagnosis.—Dermal armor reduced to a nasal plate, a jugular plate, scattered small dermal plates along the body and along the clavus. Premaxillary and dentary beaks reduced nearly to totally toothless condition with only a few, isolated, scattered teeth present along the internal beak margin. Palatal bony brace for the teeth totally reduced to cartilage.

Range.—Upper Middle Miocene to Holocene.

Osteologically, the three living and fossil species of *Mola* can be defined as follows:

Mola mola (Linnaeus, 1758)

Species diagnosis.—In addition to the generic characters, 8 to 9 ossicles along the clavus, paraxial pair of ossicles fused. Premaxillary beak strongly reduced.

Range.—Holocene.

Mola ramsayi (Giglioli, 1883)

Species diagnosis.—In addition to the generic characters, 12 ossicles along the clavus, paraxial pair not fused. Dentary and premaxillary beaks not described, presumably as for *M. mola*.

Range.—Holocene.

Mola chelonopsis (Van Beneden, 1883)

Species diagnosis.—Premaxillary beak toothless, and lacking palatal tooth brace, toothless shelf anterior to location of the former tooth position much longer than in *M. mola*, such that the antero-posterior beak length is greater than the lateral beak width at the level of the back of the shelf. Dentary beak comparable to *M. mola*.

Range.—Upper middle Miocene to lower Pliocene.

Remarks.—All but one of the premaxillary beaks which Leriche (1926) described totally lack both the bony mass above the mouth roof and the rows of

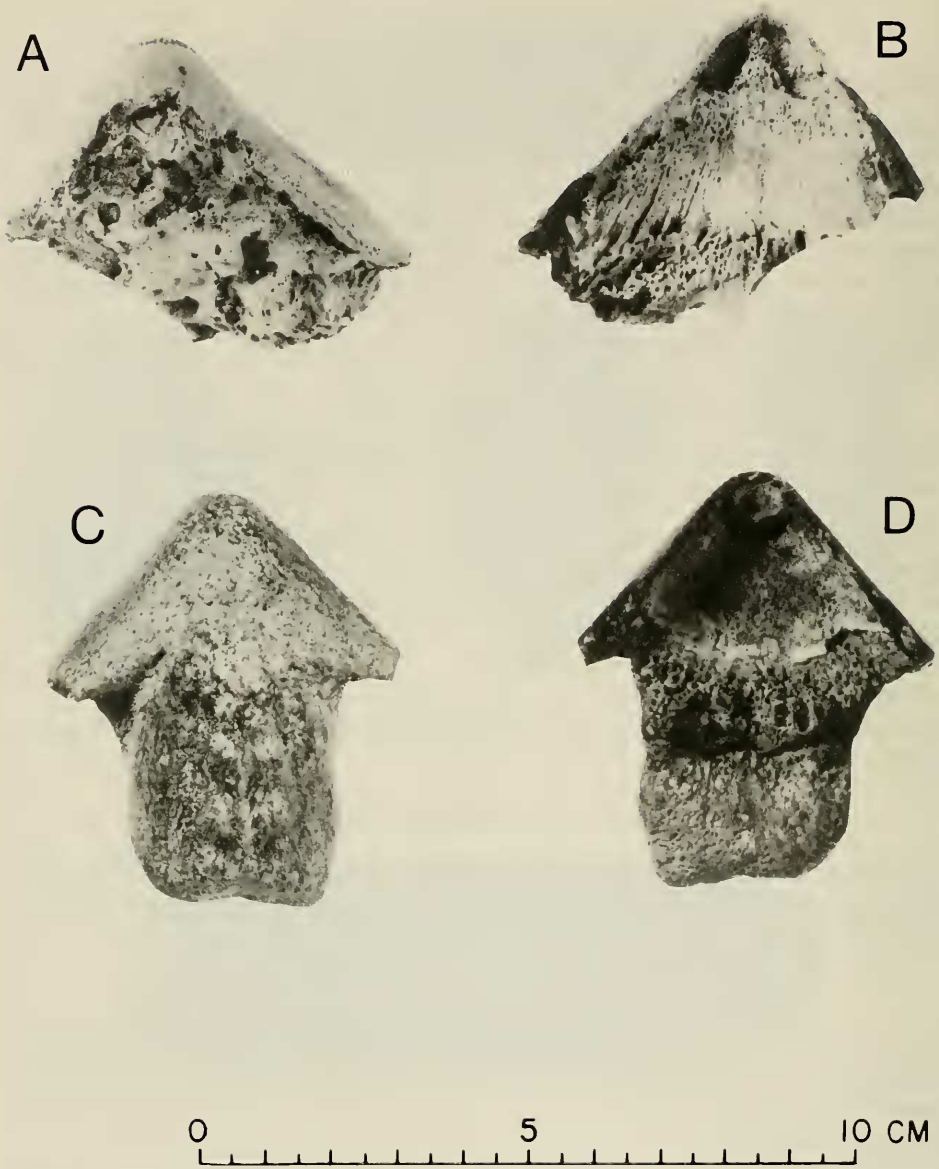


Fig. 6. Dorsal and ventral views of the premaxillary jaw of *Ranzania grahami* and *Mola chelonopsis*. A, *Mola chelonopsis* (USNM 265650), dorsal view; B, *Mola chelonopsis* (USNM 265650), ventral view; C, *Ranzania grahami* (USNM 265395), dorsal view; D, *Ranzania grahami* (USNM 265395), ventral view.

teeth. These specimens therefore should be referred to the above species. All of these specimens presumably came from the upper middle Miocene. One small beak that Leriche described has two (but not three) tooth rows imbedded in a bony palate. In the number of tooth rows present it is somewhat different from

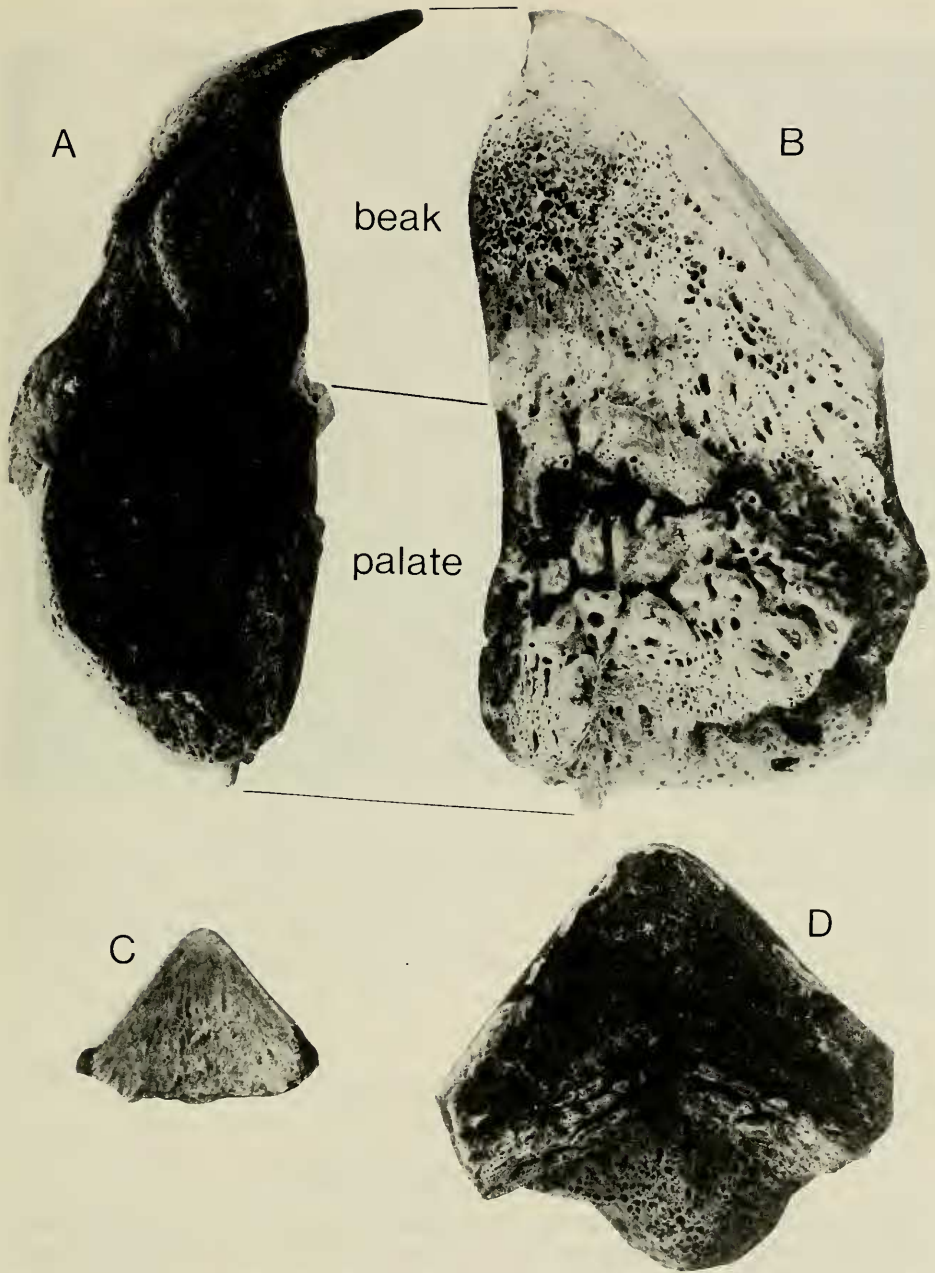


Fig. 7. The premaxillary jaws of *Ranzania tenneyorum*, *Ranzania grahamsi* and *Mola chelonopsis*. A, Midline section through a beak of *Ranzania grahamsi* (USNM 265391); B, Ventral view of same beak of *Ranzania grahamsi* showing poorly developed and irregularly placed teeth on the bony palate; C, Ventral view of beak of *Mola chelonopsis* (USNM 186983) lacking development of a bony palate. Total length 23 mm; D, *Ranzania tenneyorum* (USNM 265392) showing three well developed pairs of tooth rows on the bony palate. Total length 25 mm.

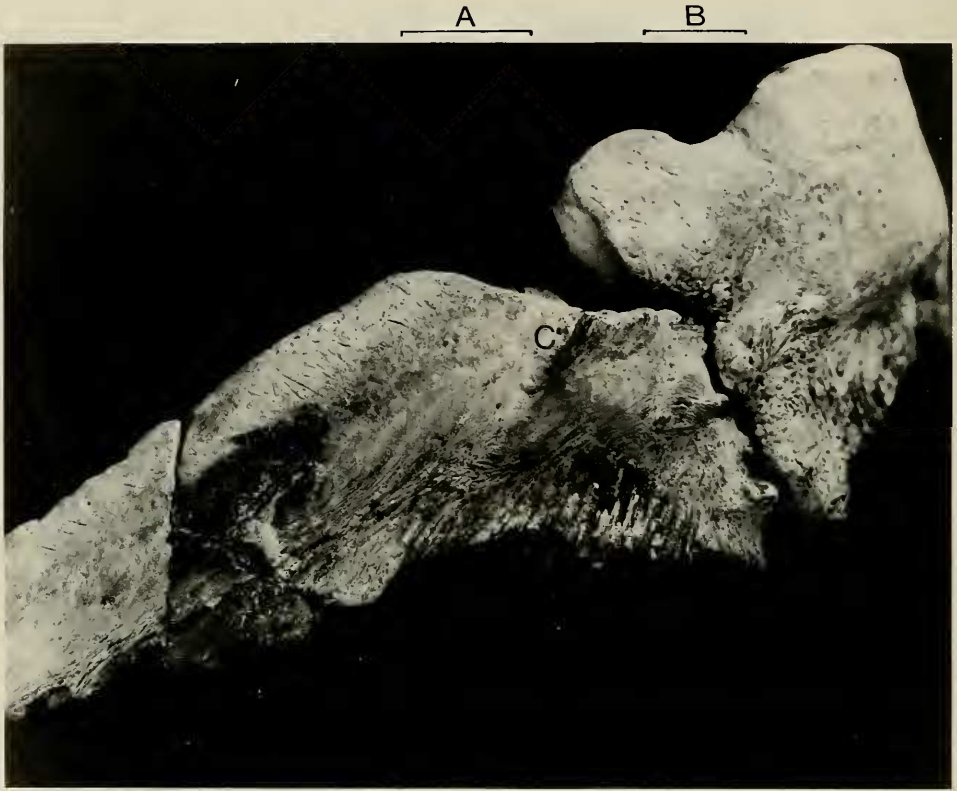


Fig. 8. Lateral view of the right dentary of *Ranzania grahami*, showing a partially healed fracture running down from a wedge shaped groove (A) produced by the tooth of an attacking predator. Although the wound partially healed, jaw occlusion was permanently altered. As a result, the premaxillary beak margin cut a broad U-shaped notch into the dentary element (B). The dark, linear shadow to the right and below "C" is a second fracture line which healed. Both the healed and unhealed fracture lines are visible in Plate 1B, because the triangular bone fragment lying between them was displaced outward at the time of injury.

R. tenneyorum, but otherwise it is similar to that species and thus probably should be assigned to it.

Phylogeny of the Family Molidae

The Calvert and Choptank specimens suggest that the genus *Mola* was derived from a form like *Ranzania tenneyorum* by way of *R. grahami* and *Mola chelonopsis* (Fig. 2). *Ranzania tenneyorum* is both morphologically and temporally a suitable ancestral form for the living *Ranzania laevis*, even though no specimens of intermediate age are known. Thus, the genera *Mola* and *Ranzania* can be closely linked by intermediate fossil forms. The crushing dental apparatus of *Masturus*, on the other hand, is quite different and suggests that *Masturus* has a more remote affinity with both *Ranzania* and *Mola*. The family Molidae is considered to be derived from a distant common stock with the mollusc-eating family Diodontidae and to be most closely related to the family Triodontidae (Tyler

1980). While different in detail, the dental apparatus of *Masturus* more closely approaches the dental apparatus of these related families than the dental apparatus of either *Ranzania* or *Mola* within its own family. Moreover, only *Masturus* retains the primitive characteristic of a vestige of the true tail, which has been eliminated totally in the other two genera and been replaced functionally by the dorsal and anal fins, and the clavus (Fraser-Brunner 1951). Therefore, it seems most likely that *Masturus* separated from the *Ranzania-Mola* stock before the appearance of the Miocene species *R. tenneyorum* and *R. grahami*, perhaps as early as Oligocene time. This indicates relationships within the family as shown in Fig. 2. Working only with modern material, Raven (1939b), Fraser-Brunner (1951), and Tyler (1980) suggested that *Mola* and *Masturus* were the more closely related living genera. Fraser-Brunner considered *Ranzania* to be the most generalized genus, while Raven and Tyler considered it to be the most derived. While I agree with Fraser-Brunner and Tyler that *Ranzania* is the most derived member of this family, the fossil sequence used for this study suggests that the gene pools of *Ranzania* and *Mola* became isolated from each other at a time later than when both became isolated from *Masturus*. This leads me to argue: 1) that the highly cartilaginous state of *Mola* and *Masturus* is the result of parallel evolution; 2) the tail remnant and dental apparatus of *Masturus* represent uniquely retained primitive features within the family; and 3) the numerous similarities between *Mola* and *Masturus* are commonly retained primitive familial characters that cannot be used to prove an especially close relationship between these two genera. This implies that the elongate and dorso-ventrally flattened body form of *Ranzania* (Fig. 2) is a derived character within this family (as Fraser-Brunner 1951, also pointed out), in contrast to the body form of *Mola* and *Masturus* which represent the primitive family character. The fact that the mouth of *Ranzania* closes along a vertical line, rather than along a horizontal line as in most vertebrates (Fraser-Brunner 1951), clearly shows that it has undergone unique specializations relative to the other genera in its family and is not simply a primitive and conservative member of this group. Therefore, it is reasonable to argue that the body shape of *Ranzania* also is a specialized rather than a primitive trait. On the basis of morphology alone, *Mola* and *Masturus* are similar, but this is believed to have resulted from persistent conservatism in these two genera rather than from an especially intimate phylogeny.

If the above phylogeny is accepted, then a graded series of evolutionary steps can be postulated to derive the living pelagic *Mola mola* (and *M. ramsayi*?) from a bottom-dwelling, molluscivorous ancestor. While the dental apparatus of *Masturus* is similar to that of the mollusc-eating Diodontidae, its body is not so rounded as that of most persistent bottom dwellers and catch records also suggest a world-wide pelagic distribution. Its known diet includes seaweed (Palmer 1936) as well as sponges, mollusks, and annelid worms (Yabe 1950). Yabe considered this diet to indicate that these fish normally feed on the sea beds. This implies that the first step in the derivation of this family was a change of feeding habit from gathering sea bed bivalves to foraging for food along the sea floor. This resulted in a major modification of the body from relatively wide and flattened to relatively narrow and high. In the line leading to modern *Ranzania*, the fish became specialized and adopted a diet that no longer included meat and consisted entirely of seaweed (Barnard 1927). This resulted in a change in the dental ap-

paratus from a crushing dentition to a shredding dentition like that found in *R. tenneyorum*. In the other, less specialized branch of *Ranzania* (*R. grahami*) leading toward the modern *Mola*, the fish became adept at eating both plants and animals. The modern *Mola* has been reported to eat algae (Bigelow and Welsh 1925; Breder 1932; Fries *et al.* 1895), seaweed (Breder 1932; Reuvens 1897; Townsend 1918), eelgrass (*Zostera*) (Bigelow and Welsh 1925; Fries *et al.* 1895; Reuvens 1897), sponges (Breder 1932), hydroids (Bigelow and Welsh 1925), jellyfish (Bellomy 1961; Bigelow and Welsh 1925; Binney 1842; Breder 1932; Dieuzeide *et al.* 1955; Fries *et al.* 1895; Hargitt 1905; Hubbs and Schultz 1929; Linton 1901; MacGinitie and MacGinitie 1949; Nichols and Breder 1927; Zimbelman 1967), ctenophores (Bigelow and Welsh 1925; Hargitt 1905; Linton 1901), mollusks (Bigelow and Welsh 1925; Dieuzeide *et al.* 1955; Fries *et al.* 1895), crustaceans (Bigelow and Welsh 1925; Dieuzeide *et al.* 1955; Fries *et al.* 1895; Linton 1901; Nichols and Breder 1927), echinoderms (Bigelow and Welsh 1925), salps (Bigelow and Welsh 1925; Dieuzeide *et al.* 1955; Fries *et al.* 1895; Linton 1901; Nichols and Breder 1927), and fish (Boulenger 1936; Dieuzeide *et al.* 1955; Fraser-Brunner 1951; Fries *et al.* 1895; Grassi 1897; Norman 1931; Norman and Fraser 1949; Reuvens 1897; Schmidt 1921). This kind of a diet only requires a dental apparatus for plucking and swallowing. This set the stage for the nearly total loss of palatal teeth and their supporting bony shelf that has occurred in *Mola*. Thus the morphological changes that can be seen in the premaxillary beak, from *Ranzania tenneyorum* through *R. grahami* and *Mola chelonopsis* to *M. mola* and *M. ramsayi*, are interpreted here to reflect a progressive change in the habitat and diet of these forms.

Pathology

The type-specimen of *Ranzania grahami* (USNM 186986) has a broad notch in the dentary beak. Below this notch two radiating fractures are present. One fracture is completely knit but the other is not, even though a great deal of bone growth has occurred in the vicinity of the fracture (Figs. 3A, B, 8). This is obviously a pathological condition perhaps resulting from an attack by a large predator. The partial healing of the fracture indicates that the victim survived for an extended period of time, as does the strongly asymmetrical wear on the dentary beak tip and the presence of a deep wear-notch cut into it by the premaxillary beak (Fig. 8). The notch facet and wear pattern clearly show that jaw occlusion was severely distorted by the attack, and the fact that the animal survived at all suggests that it could swallow food whole without complex mastication. This suggests that *R. grahami* was far along in its feeding habits towards handling a *Mola*-like rather than a *Ranzania*-like diet. It is interesting to note that the osteological response to this wound was similar to that seen in untreated human fractures; i.e. formation of bony masses around the persistently unknit fracture.

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United States Geological Survey, Mail Stop 928, Reston, Virginia 22092.